The development of the spikelets of Zea Mays

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(WITH PLATE 23 AND THIRTY-THREE TEXT FIGURES)

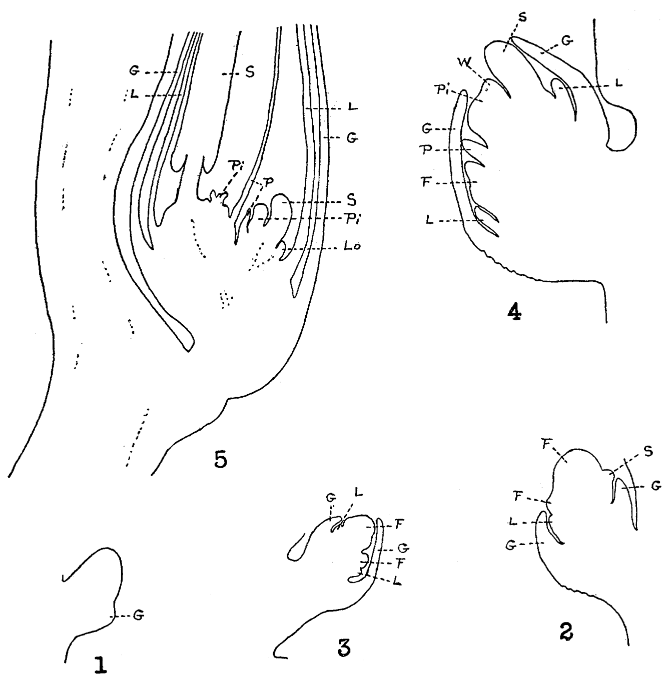
In another publication (8) a description has been given of the flowers of maize, in which the chief emphasis was laid upon the more conspicuous floral features at the time of anthesis. The writer's present purpose is to consider the two types of spikelet from the standpoint of development.

A number of articles have touched upon this subject incidentally, but in no case completely, having in nearly every case something else as their main purpose. True (7) has given a description of the formation of the pistil and the ovule in so far as this is of help in explaining the development of the caryopsis. Poindexter (6) gives a preliminary report on some work of the same kind with corn, but, if the work has ever been completed and published in full, I have no knowledge of it. Guignard's investigations on double fertilization in maize added some information, but his paper (3) naturally does not describe fully the development of the spikelets, and it is not illustrated. Goliński (2), basing his work upon *Poa annua* and *Triticum vulgare*, has given the most comprehensive treatment that I have been able to find of floral development in the grasses; this includes a good account of the literature on the subject up to that time. No reports that I have investigated have taken into account the development of the various rudimentary organs of the spikelets.

During the last four years I have had under observation in one way or another more than a hundred varieties of maize, which have been received from many parts of North and South America and may be considered a fair representation of the species. Of course, not all of these have been examined in detail, but any variety that seemed to be different from the typical in floral development was made the subject of special study until the nature and significance of the variation were determined. Monoe-

cism is the rule in almost all varieties, and the behavior of the floral organs, either functional or rudimentary, is fairly constant. This monoecious form is taken as the type for the purpose of description, and those varieties having a large proportion of perfect flowers, together with the numerous instances of reversion are mentioned only as aids in understanding the typical form.

The development of either of the typical unisexual spikelets of maize can best be described by comparison with a theoretical primitive spikelet such as occurs in some varieties of pod corn, and the like of which is found in several other grasses. This



FIGS. 1–5. Development of the male spikelet, × 60. *G*, glume; *L*, lemma; *F*, flower primordium; *S*, stamen; *P*, palea; *Pi*, pistil; *Lo*, lodicule (in a portion of the section that is not median); *W*, ovary wall.

spikelet has two empty glumes and two flowers with four palets. Since the bracts have an alternate arrangement on the rachilla, one flower is a little higher than the other in the spikelet. The higher one, which is on the side of the spikelet toward the rachis, is the older. Each flower has a pistil, three stamens, and two

lodicules. It will be shown that the present maize spikelet, whether male or female, has essentially the structure of this primitive one with some of its parts suppressed.

The spikelet primordium makes its appearance as a rounded protuberance on the rachis. The first differentiation to appear is in the formation of the lower glume, and it is soon followed by the upper one (*G*, TEXT-FIGS. 1, 6, 7). The two lemmae arise almost simultaneously with the appearance of the stamens of the upper flower (*L* and *S*, TEXT-FIGS. 2, 3, 8). From the lower side of the undifferentiated part of the spikelet now appears the primordium of the lower flower (*F*, TEXT-FIGS. 3, 4, 8), and the palea of the upper flower soon follows (*P*, TEXT-FIG. 9). The palea of the lower flower appears much later (*P*, TEXT-FIGS. 5, 10). The older flower *seems* to be terminal and the younger one lateral on the rachilla, but it is probably better to consider both flowers lateral branches of this axis, which terminates between the two paleae. This point, however, should be investigated further.

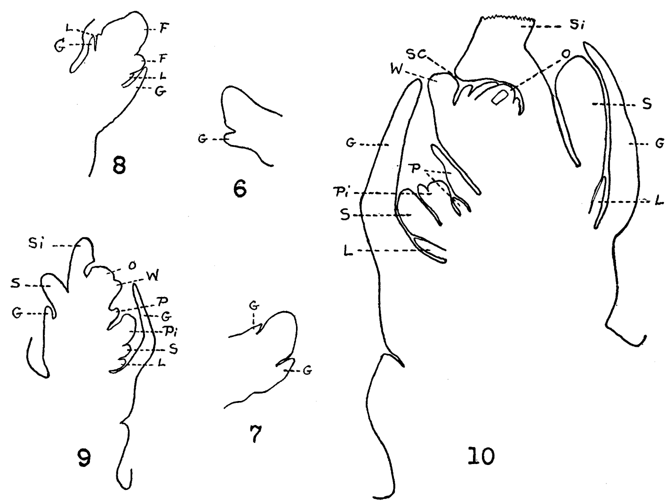
In the development of the flower from its primordium the stamens are first differentiated; these are followed by the lodicules and the part that is left is the primordium of the pistil.

Up to the time of the differentiation of the primordia of the stamen and the pistil, the male and female spikelets have looked very much alike, but now, accompanying the sexual differentiation, there begins a divergence in the appearance of the two. The covering of husks for the female inflorescence, the effects of crowding, etc., bring about further changes until the male and female spikelets finally resemble each other so little that there is a current doubt, or ignorance, at least, of their homologies.

In both flowers of the male spikelet the stamens and lodicules are fully developed, but the development of the pistils is soon arrested, and they disorganize.

The lodicules begin as small protuberances and develop into thick, short, truncated bodies. They are well supplied with vascular tissue and at anthesis are quickly distended to two or three times their former width, very efficiently holding open the spikelet while the filaments of the stamens are elongating. The development of the stamen does not differ very much from that in other grasses. Cross sections of anthers just before the time of the

reduction division (PLATE 23, FIG. 4) show the typical parts as described by Golinski, and these, except the epidermis, are practically all absorbed by the time the pollen is mature. For the greater part of the length of the anther its wall consists of merely the epidermis (FIG. 5), but for a short distance at the distal end this wall is reinforced by the mechanical layer (FIG. 6). As a



FIGS. 6–10. Development of the female spikelet, × 60. *G*, glume; *L*, lemma; *F*, flower primordium; *S*, stamen; *P*, palea; *Pi*, pistil; *Si*, silk; *O*, ovule; *SC*, stylar canal; *W*, wall of ovary.

result, it is only at the end of the anther that the loculi coalesce in pairs to form the two "cells," and the opening is a pore formed by the turning back of the edges of a short slit extending along the anther as far as the mechanical tissue goes (FIG. 7). From this pore the pollen grains escape as the wind moves the anther about at the end of the long filament.

The reduction division and maturation of the pollen do not furnish very satisfactory material for cytological work. The chromosomes are small and hard to differentiate clearly in the dense cytoplasm. Kuwada (4 and 5) has made a cytological study of a number of varieties and concludes that there is considerable variation in the size and number of the chromosomes. The haploid number in most varieties of sweet corn is found to be twelve, and in other varieties the number is often smaller. To

one who is familiar with the plant in its other interesting relations, Kuwada's work, while of much value as far as it goes, is still incomplete. There is yet room for a great deal of interesting and profitable cytological work on varieties that have been inbred for a number of generations, or whose genetic history is otherwise known for a long time. If from such work any regularity can be found for the different varieties, there will be afforded not only a probable basis for improving the present unsatisfactory systematic treatment of the genus but also a new field of study in correlations between cytological behavior and genetic results.

The mature pollen grain is almost spherical; the exine is minutely roughened, and there is a prominent germ pore (FIG. 8). The pore is surrounded by a thickened ring of intine and closed with a plate of tissue which resembles the rest of the wall in structure. The protoplasm is very dense, and careful staining is necessary to make the nuclei visible. The vegetative nucleus is irregular in outline and apparently does not have a definite membrane. The generative nucleus divides before the pollen is shed, forming the two long, slender sperms, which are pointed at the ends and usually crescent-shaped.

It is possible that the development of the abortive pistil varies in some kinds of maize, especially some of the pod varieties that do not produce fruits in the tassel; but there is a remarkable regularity in all that I have examined. The organ develops as in the female flower—which will be described later—up to the time when the ovary wall should begin to be formed, but here it stops. Sometimes it is merely an oval or somewhat constricted protuberance (TEXT-FIG. 12), and sometimes there is a slight indication of the beginning of the ovary wall (*W*, TEXT-FIG. 4). In a few cases a large, conspicuous cell has been seen at about the place where the megaspore mother cell would be expected, but it is impossible to say at this time whether or not it develops this far. The disorganization begins while the epidermis is still intact and soon extends to many or all of the intercellular spaces (TEXT-FIGS. 12–15). The organ is usually completely consumed by the time of the differentiation of the pollen mother cells in the stamens of the same flower, and all that remains at anthesis is a small, shallow cup formed by the epidermis of the base of the aborted organ

(TEXT-FIGS. 5, 15). This is so inconspicuous that it appears that many early investigators, working largely from the systematic

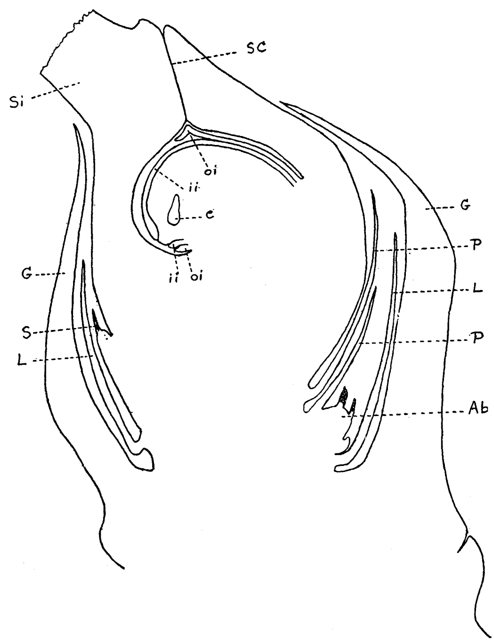


FIG. 11. Longitudinal section of female spikelet, × 60. *G*, glume; *L*, lemma; *P*, palea; *Ab*, aborted flower; *Si*, silk; *SC*, stylar canal; *e*, embryo-sac; *oi*, outer integument; *ii*, inner integument.

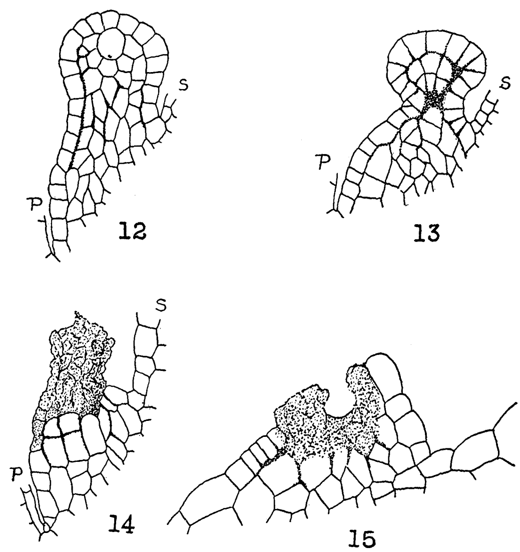
standpoint, either did not suspect its presence, or looked for it and failed to find it.

The female spikelet is characterized by a suppression of all the essentials of the lower flower and of the stamens of the upper one. Lodicules are present in both flowers, but they are functionless, or, at least, do not serve the same purpose as in the male flower. The only functional organ of the female spikelet is the pistil of the upper flower.

The lodicules of both flowers of the female spikelet are, in early stages, like those of the male flower, but their development is arrested at about the same time as that of the other rudimentary parts. This suppression is not accompanied by disorganization, as in other parts, but the organs merely stop growing and are wholly or partly overtaken by the growth of the surrounding

tissues. At anthesis those of the upper flower are seldom visible, while those of the lower flower are relatively conspicuous even when such flower has a functional pistil.

The pistil of the upper flower is not materially different from that of other grasses. Guignard's description is accurate. As



FIGS. 12–15. Sections showing steps in the decline of the pistil of the male flower, × 60.

he has pointed out (3, p. 43), the pistil seems to be developed from a single carpellary leaf. The duplex structure of the "silk" indicates that it may have resulted from the union of two parts, but there is no direct evidence of this.

After the stamen primordia have been differentiated, the beginning of the pistil is left as a small, rounded protuberance. Near the base of this a ring of tissue begins to grow up and finally arches over to form the ovary wall (*W*, TEXT-FIGS. 9, 10, and PLATE 23, FIG. 3). Ultimately the edges of this come together at the top, but the union is never complete, a small opening to the inside, the stylar canal, being present at the top of the mature ovary (*SC*, TEXT-FIGS. 10, 11). In the meantime, a small projection grows up on the adaxial side of the stylar canal, a little distance from the latter, to form the primordium of the "silk."

The "silk," which is peculiar to maize and teosinte, probably owes its unusual structure and exceptional length to the presence of the husks that cover the inflorescence. The writer has previously called this organ a stigma. Since the use of this term has been questioned, a further statement seems appropriate here. The difficulty seems to lie in finding a consistent and generally accepted definition of the word, *stigma*. Some writers, as Strasburger and a number of his students, speak of it as a morphological unit of the pistil, coördinate with the style and the ovary; and others define it as merely that portion of the surface of the style upon which pollen grains may germinate. In dealing with the grasses it is convenient to speak of the feathery part of the filament extending upward from the ovary as the stigma and of the smooth part as the style. Strasburger makes this distinction in his text book. Many other writers, in describing the grasses, recognize the convenience of such a distinction when they speak of the "two or three feathery stigmas." It was not, and is not now, the writer's intention to form a new definition of terms. The point intended is merely this: The corn silk, being compound in structure and plumose and receptive to its base, is the homologue of the "two feathery stigmas" of other grasses. If the common use of the word, *stigma*, in speaking of other grasses is inadvisable, and a consistent nomenclature is devised, the appropriate use of the word, *style*, for the corn silk is conceded.

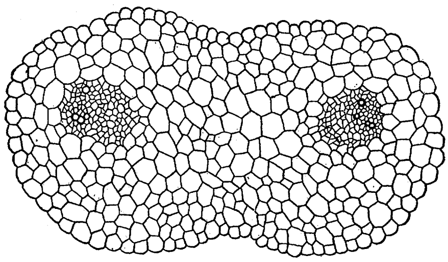
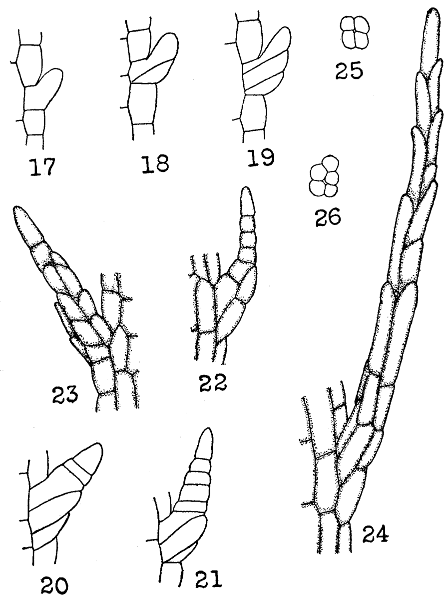


FIG. 16. Transverse section of the silk, × 200.

From the very beginning (PLATE 23, FIG. 3) the silk is divided at the tip, and this division continues into the mature structure, which has already been described (**8**, p. 133). Two strands of vascular tissue traverse the entire length of the organ (TEXT-FIG. 16). Neither in transverse nor in longitudinal section is there any evidence of a tissue morphologically differentiated for the passage of the pollen tube, as has been described for other grasses.

The plumose appearance of the stigma is due to numerous

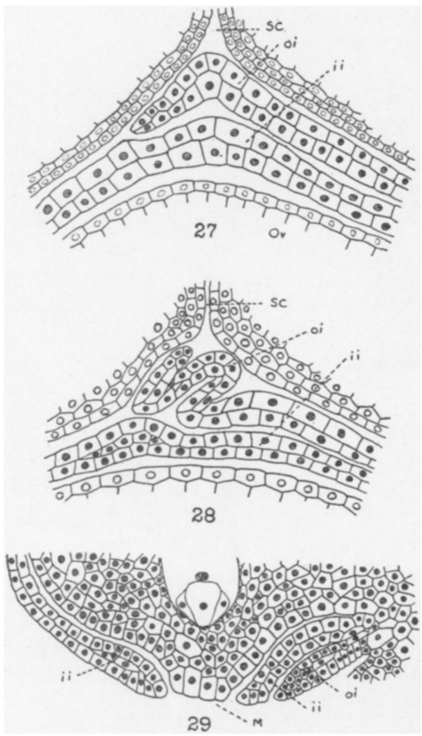
hairs arranged in definite areas. Each hair has its origin in a single epidermal cell (see TEXT-FIGS. 17–24) which divides anticlinally, giving rise to four, or occasionally five, cells. Each of these cells divides transversely a number of times and produces a long filament, the four filaments being loosely attached to each other, leaving an intercellular canal in the middle of the hair. Some of the filaments are longer than others, and, as a result, the hair tapers to a point, where it consists of but a single cell or a single row of cells. The upper ends of many cells of the hair are turned outward, giving the pollen tube easy access to the canal in the middle (TEXT-FIG. 25), through which the tube reaches the main part of the silk. It seems that it is only through these hairs that the pollen tube can gain entrance.



FIGS. 17–24. Steps in the development of a stigma hair. FIGS 25 and 26. Cross sections of stigma hairs, × 200.

The ovary contains a single ovule, which is of a modified campylotropous form. At about the time of the differentiation of the megaspore mother cell, the integuments begin to grow up around the nucellus. The tissues on the adaxial side of the ovule grow so much faster than those on the other side that, at time of the maturity of the embryo sac, that organ, with the tissue immediately surrounding it, has been completely inverted. The ovule is attached for a considerable distance along one side, and no funiculus is present; the embryo sac remains straight, as does the developing embryo. The one part of the outer integument seldom grows further than the top of the ovary, where it forms a folded or wedge-shaped body, closing the stylar canal (TEXT-FIGS. 27, 28). The micropyle is formed by the inner integument, and the nucellus protrudes through it (TEXT-FIG. 29).

The peculiar details of the embryo sac of the grasses have long been know, as Goliński (2) shows in his review of the literature. In the early stages of development it is not unlike that of many other angiosperms. I have found in the case of *Zea Mays* no evidence of the disorganization of any of the megaspores, and it is probable that all four function as in the group of plants of which *Lilium* is the classical type.

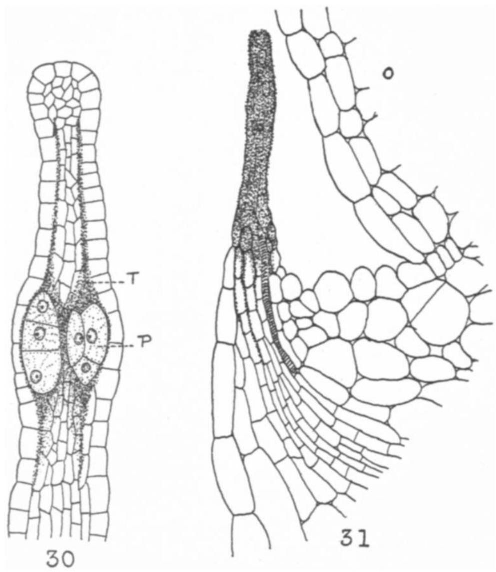


FIGS. 27 and 28. Outer integument and stylar canal. FIG. 29. Micropyle, × 150. *SC*, stylar canal; *oi*, outer integument; *ii*, inner integument; *Ov*, ovule; *M*, micropyle.

In cytological details I have found nothing in conflict with Guignard's description (3, p. 44) of the mature embryo sac, and only those details will be repeated in which there is some significant peculiarity. After the organization of the embryo sac the antipodals divide until there are a large number of cells—sometimes twenty-five or more—some of which have more than one nucleus (PLATE 23, FIG. 1). The polar nuclei do not fuse before the fecundation of the egg.

The abortive stamen of the upper flower of the spikelet develops in the same manner as the functional one of the male spikelet up to the formation of the pollen mother cells; but the loculi are much smaller, and the pollen mother cells fewer than in the normal stamen. Disorganization begins in the tapetal region, and the pollen mother cells are consumed before the epidermis is affected (TEXT-FIG. 30). At anthesis these stamens are small, inconspicuous, disorganized appendages near the base of the pistil (TEXT-FIGS. 11, 31).

The fate of the parts of the lower flower of the female spikelet is similar to that of the homologous aborted parts of the other flowers. TEXT FIG. 33 shows a section of the flower at the time

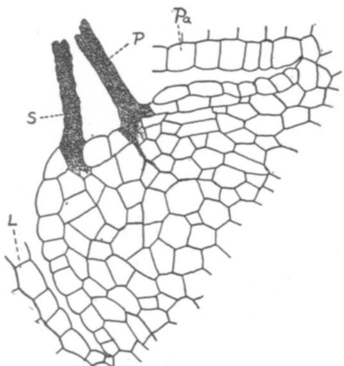


FIGS. 30 and 31. Disorganization of the stamen in the female flower, × 200. *T*, tapetal region; *P*, pollen mother cells; *O*, ovary.

of its highest development, the pistil having already begun to decline. So far as has been determined, no spore mother cells are formed in either the stamens or the pistil. It seems that the decline of all the suppressed organs of the female spikelet begins simultaneously, or nearly so, and the difference in age between those of the upper and those of the lower flower would account for the difference in the degree of development finally reached. These organs of the aborted flower are finally reduced to the condition of the other aborted pistils and stamens, and at anthesis the lodicules are the only prominent parts of the flower. As has already been noted (**8**, p. 135), the pistil of this flower is known to function with more or less regularity in some varieties.

The cause of this suppression of some organs in all spikelets, resulting, as it does, in monoecism, is unknown. But the fact that variations to the perfect-flowered condition sometimes occur

temporarily in strains that have for a long time been monoecious in character, and that these reversions are, in a measure, capable of experimental control, offers a good field for the physiologist. Some of the work of Blaringhen (1) evidently has such facts as



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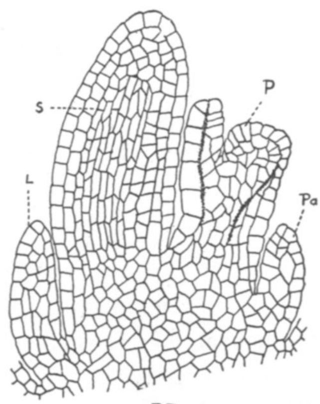

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FIG. 32. Lower flower of the female spikelet beginning to be disorganized, × 200. FIG. 33. Aborted flower of the female spikelet at the time of anthesis, × 200. *S*, stamen; *P*, pistil; *L*, lemma; *P*, palea.

these as its basis. It is a noteworthy fact that the organs that are to be suppressed develop normally up to the point where rapid growth and sexual development begin, and then rapidly decline, and this suggests a lack of adequate nutrition. But, before proceeding far on this supposition, we must consider two significant facts: In either the ear or the tassel, there is a strict regularity in the selection of the sex to be suppressed; and it is by starving the whole plant, as when it is grown in a pot in the greenhouse in the winter, that perfect flowers in the tassel are likely to be produced.

SUMMARY

The spikelets of all varieties of maize begin to form two perfect flowers, and monoecism is caused by the suppression of some part or parts of all the flowers. The entire lower flower of the ear spikelet is suppressed, except in a few varieties, and ordinarily only one fruit develops.

In any single flower the development of the stamens is more

advanced than that of the pistil; but the pistil of the upper flower of a spikelet is usually more advanced than the stamens of the lower flower.

In the organs in which it occurs, suppression begins at about the time of the differentiation of the spore mother cells in the functional organs.

The aborted stamen of the functional female flower produces microspore mother cells before it begins to decline, and the aborted pistil of the male flower may produce a megaspore mother cell, but the organs of the aborted flower of the female spikelet do not produce spore mother cells.

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Explanation of plate 23

FIG. 1. Embryo sac, *E*, egg; *SS*, synergids; *P*, polar nuclei; *A*, antipodal tissue.

FIG. 2. Another section of the embryo sac shown in Fig. 1.

FIG. 3. Very young pistil, × 60. *S*, one lobe of silk; *W*, beginning of ovary wall.

FIG. 4. Section through the middle of an anther just before the reduction division, × 50.

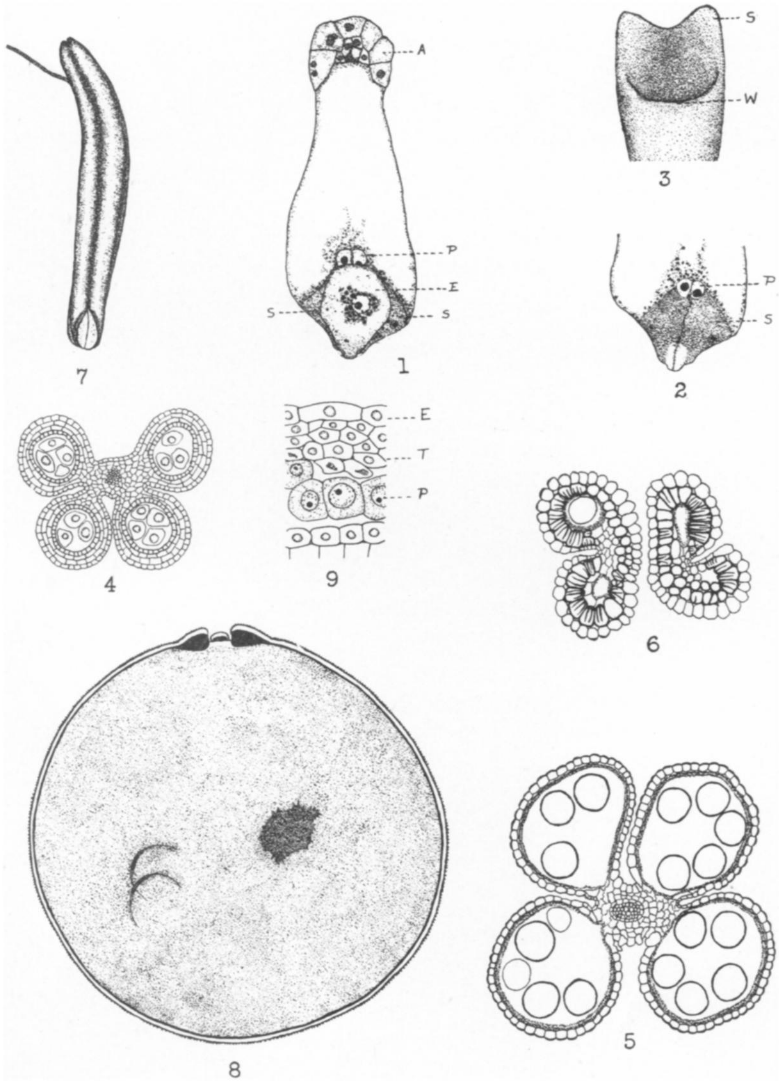
FIG. 5. Section through the middle of a mature anther, × 50.

FIG. 6. Section from near the distal end of the anther shown in FIG. 5.

FIG. 7. A mature anther, × 10.

FIG. 8. Section of pollen grain, showing germ pore, vegetative nucleus, and the two sperms, × 550.

FIG. 9. Portion of a longitudinal section of a stamen of the female flower, just before disorganization begins, × 200. *E*, epidermis; *T*, tapetal region; *P*, pollen mother cells.



WEATHERWAX: SPIKELETS OF ZEA MAYS